BRAGE/IMR

Brage IMR –

Havforskningsinstituttets institusjonelle arkiv

Dette er forfatters siste versjon av den fagfellevurderte artikkelen, vanligvis omtalt som postprint. I Brage IMR er denne artikkelen ikke publisert med forlagets layout fordi forlaget ikke tillater dette. Du finner lenke til forlagets versjon i Brage-posten.
Det anbefales at referanser til artikkelen hentes fra forlagets side.

Ved lenking til artikkelen skal det lenkes til post i Brage IMR, ikke direkte til pdf-fil.

Brage IMR –

Institutional repository of the Institute of Marine Research

This is the author's last version of the article after peer review and is not the publisher's version, usually referred to as postprint. You will find a link to the publisher's version in Brage IMR. It is recommended that you obtain the references from the publisher's site.

Linking to the article should be to the Brage-record, not directly to the pdf-file.

HAVFORSKNINGSINSTITUTTET
INSTITUTE OF MARINE RESEARCH

Foto: Leif Nøttestad

Fecundity and growth of Atlantic cod (*Gadus morhua* L.) along a latitudinal gradient

Anders Thorsen[a*], Peter R. Witthames[b, 1], Gudrun Marteinsdóttir[c], Richard D.M. Nash[a], Olav Sigurd Kjesbu[a]

[a]Institute of Marine Research, P.O. Box 1870 Nordnes, 5817 Bergen, Norway
[b]Centre for Environment, Fisheries & Aquaculture Science (Cefas), Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk NR33 0HT, England, United Kingdom
[c]Institute of Biology, University of Iceland, Sturlugata 7, 101 Reykjavik, Iceland

*Corresponding author. Tel.: +47 55238444; fax: +47 55238531

[1]Present address: Fecund-Fish Consultancy, 40 Plumtrees, Lowestoft, Suffolk NR32 3JH, England, United Kingdom

E-mail addresses: anders.thorsen@imr.no (A. Thorsen), fecund-fish@tiscali.co.uk (P.R. Witthames), runam@hi.is (G. Marteinsdottir), richard.nash@imr.no (R.D.M. Nash), olav.kjesbu@imr.no (O.S. Kjesbu)

Running headline: Reproductive tactics of Atlantic cod

KEYWORDS
Cod, fecundity, atresia, maturation, temperature

ABSTRACT

Some fish species have wide distribution areas that span very different habitats. In this investigation we have studied Atlantic cod (*Gadus morhua*), which is an example of such a species, to demonstrate how this may have caused adaptations to key features such as fecundity, growth and age and size at first spawning. We have studied cod from the Barents Sea, Icelandic waters, North Sea and Irish Sea. The ovary sampling was undertaken over several years, however, not always sequentially, in order to assess whether the relationships between fecundity and other key features were constant or variable. Also, we compared historical maturity ogives and growth from the different regions. There was a clear pattern with fish maturing at a greater age and size in the north compared to the south. For three of the four cod stocks we demonstrated a significant reduction in relative potential fecundity as maturity progressed towards spawning, i.e., as the mean diameter of vitellogenic follicles increased. To be able to compare potential fecundity in a standardised way both in time and space, we constructed models that included mean diameter as one of the independent variables. Our potential fecundity comparisons clearly indicated a north-south gradient with increasing size-specific fecundity towards the south. The higher fecundity of the fish in the south could only partly be explained by the higher condition and temperature that was observed in these waters.

1. Introduction

Successful reproduction depends on the adaptation of reproductive physiology and behaviour of the animal to its environment. Different species of fish have often evolved intriguing reproductive strategies that reflect local adaptation to surrounding environmental conditions and ecological niches (Murua and Saborido-Rey, 2003). As a result, extensive variation characterizes all reproductive traits, such as the timing, frequency, duration and amplitude of spawning as well as offspring size and numbers (Wootton, 1998; Wright and Trippel, 2009). The size and number of eggs and larvae produced by individual fish are therefore determined by the predictability of survival and trade-offs in energy allocation to reproduction, growth, behaviour and maintenance (Smith 1974; Stearns, 1992; Roff, 2000). The reproductive strategies range from spawning once to a number of times either in a single spawning season or over many (semelparous versus iteroparous), through a range in synchrony and when fecundity is determined (determinate versus indeterminate fecundity) to variations in

the spawning pattern (total versus batch spawners). In addition, there is a wide range in egg size between species with smaller, but perceptible differences within a species, which can be regarded as a trade-off between size and number (Wootton, 1998). Within a widely distributed species, such as the Atlantic cod (*Gadus morhua*) (Fig. 1), these traits are likely to be plastic and vary extensively among populations that inhabit different environments (Stearns, 1992, 2000; Rowell, 1993; Yoneda and Wright, 2004).

In this paper we focus on four cod stocks, i.e., the ones in the Barents Sea, SW Icelandic waters, the North Sea and the Irish Sea. These are distributed over a wide range of environment with annual mean temperatures, at 100 m depth, ranging from 4 °C in the Barents Sea to around 10 °C in the Irish Sea (ICES, 2005; Sundby, 2000; Sundby and Nakken, 2008). In addition to temperature, these stocks are likely to differ in many ways due to adaptation to different feeding conditions, predation, fishing mortality, probability of offspring survival as well as energy invested in reproductively associated behaviour such as spawning migrations. The Barents Sea cod typically have a very long spawning migration along the Norwegian cost to spawn at the coast of Finnmark, Lofoten, or even further south (Bergstad et al., 1987; Jørgensen et al., 2008). The distance of migration practised by the Icelandic cod stock can vary from being quite far for those that migrate from Greenland waters (Schopka, 1993) to shorter distances for those that migrate from the feeding areas of the NW or SE coast (Jonsdottir et al., 2007). The North Sea and Irish Sea stocks have shorter or even no spawning migration (Jonsdottir et al., 2007; Righton et al., 2007; Robichaud and Rose, 2004). The length of the spawning migration, and associated energy demands of each stock, depends on the spatial separation of the centre of egg and larval production compared to the adult feeding area (Harden-Jones, 1968).

A key feature amongst fish reproductive traits is the number of eggs that are shed, also called the realised fecundity. The reproductive investment can be considered as the ovarian weight or the product of realised fecundity and egg dry weight. The use of ovary weight can produce bias since weight changes for a variety of reasons through the developmental process e.g. further sequestration of yolk (vitellogenin) or oocyte hydration,; the timing of measurements is critical. Hence, the use of egg dry weights and realised fecundity will clearly provide a better estimate of the actual reproductive

investment. Unfortunately, data for egg dry weight and realised fecundity are not available for any of the stocks in this study. Therefore, potential fecundity, defined as the number of vitellogenic oocytes present in the pre-spawning fish is often taken as a proxy for reproductive investment. Indeed a central tenant of the stock and recruit relationship (Beverton and Holt, 1957) assumes that stock biomass is a suitable proxy for fecundity subject to a scaling factor. In some cases the realised fecundity is estimated from the potential fecundity by subtracting the number of atretic (regressing) oocytes found in the prespawning ovary (Armstrong et al., 2001; Greer Walker et al., 1994; Ma et al., 1998; Óskarsson et al., 2002; Witthames et al., 2003). In the case of cod significant progresses have been made in the understanding and quantification of the atresia regression turnover rate (Witthames et al., this issue) as well as in the reporting of atretic intensity (Kjesbu et al., this issue) However, these studies are either experimental or limited to specific waters.

A recent study on cod (Thorsen et al., 2006) has shown a considerable decrease of potential fecundity during the vitellogenic phase of ovary development. The work indicated that the time of sampling in the developmental process had an important influence on fecundity estimate. The authors therefore recommended that stage of maturation should be compensated for when comparing fecundities between stocks or years. Specifically they suggested that mean oocyte diameter could be used as an indication of proximity to spawning time and hence how far in the development cycle the fish has progressed and thus included as an independent factor in multiple regression analysis. Typically vitellogenesis starts at around 250 µm diameter and ends when the oocyte is 800-900 µm (Kjesbu et al., 1990; Kjesbu and Kryvi, 1993; Thorsen and Kjesbu, 2001). Finally, egg size seems to a large degree to be determined during the last 2-3 days of final maturation (development) when the uptake rate of vitellogenin is particularly large (Kjesbu et al., 1996; Wallace and Selman, 1985). Furthermore, oocytes take up large quantities of water that may increase their volume by a factor of 3-5 compared to the prehydration state (Fulton, 1898; Milroy 1898; Thorsen and Fyhn 1996,). Typical egg size for Atlantic cod seems to be in the range 1.15-1.6 mm while in an extreme case like the Baltic Sea the egg size may be up to 1.8 mm (Marteinsdóttir and Begg 2002; Thorsen et al., 1996).

In this paper we have used the proposed methods for unbiased fecundity comparison outlined in Thorsen et al. (2006) to compare cod fecundity for several stocks of Atlantic cod both in time and space. The material included data on fecundity and maturation from Barents Sea cod, Icelandic cod, North Sea cod, and Irish Sea cod together with data on length, weight, and age.

2. Methods

2.1. Age, otolith type, length, weight and maturity

For all stocks we had individual data on length, weight, and age. All cod caught were measured to the nearest 1 cm below, weighed to the nearest 1 g, the sex identified from the gonads, and the maturity stage judged macroscopically.

Maturity ogives for Barents Sea female cod were estimated from a combination of VPA and survey data. The methods are given in Nash et al. (this issue). Growth in length for Barents Sea cod was estimated from the central IMR cruise database for January - April in the years 1986-2006. Most of the cod had been caught by bottom trawl or Danish seine. Only cod containing otoliths characterized as part of the Barents Sea population (Rollefsen, 1934) were included.

Growth in length for Icelandic cod was estimated from data obtained from the public web data library (http:// www.hafro.is) of the Icelandic Marine Research Institute. These data originated from the spring research surveys and included cod caught by Danish seine and bottom trawl for all divisions in the years 1992 to 2005.

Maturity ogives and a growth curve for North Sea cod were obtained from the first quarter ICES IBTS (International Bottom Trawl Survey) in the years from 1981-2002. A standard weighting factor for each observation was calculated as the product of the number of fish that the observation represented and the inverse of the tow duration. The survey generally covered most of the North Sea but in the early 1990s included stations in the Kattegatt and Skagerrak (ICES Division IIIa). Data from IIIa were removed by excluding all samples collected east of 8^{o}E. A standard GOV trawl was used with most hauls lasting approximately 30 min. The database consisted of position and haul duration, lengths (to the nearest cm), sex, coding for mature or

166 immature, and number of fish for each entry. The methods for estimating the female
167 maturity ogives are given in Nash et al. (this issue).
168
169 Maturity ogives for Irish Sea cod in the years between 1992 – 2006 were obtained
170 from the annual Irish Sea spring groundfish survey, conducted by the Agri-Food and
171 Biosciences Institute in Northern Ireland. Growth in length for Irish Sea cod was
172 estimated from data for 2003-2005. The survey is conducted in March each year using
173 a rock-hopper otter trawl. A weighting factor for each observation was taken as the
174 inverse of the distance towed. The maturity ogive results are reported in Nash et al.
175 (this issue).
176
177 *2.2. North Sea and Irish Sea cod fecundity samples*
178 Cod were sampled between December and the beginning of March in the North Sea
179 and Irish Sea for the 2003 and 2004 spawning seasons (Fig. 1) when the cod
180 population was in the process of late maturation (vitellogenesis) and spawning.
181 Potential fecundity and size frequency distributions of vitellogenic follicles were
182 determined using the auto-diametric fecundity method (Thorsen and Kjesbu, 2001).
183 During the analyses spawning fish were identified by the presence of spawning
184 markers (hydrating follicles, hyaline eggs or postovulatory follicles) in the ovary
185 samples (whole mounts) and these were excluded from the fecundity analyses
186 (Witthames et al., 2009).
187
188 *2.3. Barents Sea cod fecundity samples*
189 Pre-spawning cod were sampled between 1987 and 2006 at Andenes (Fig. 1) as the
190 Barents Sea cod are migrating southward to the Lofoten and Vesterålen spawning
191 areas. The samples were taken from commercial landings of locally caught fish in the
192 first half of March (Kjesbu et al., 1998). Potential fecundity was determined using the
193 gravimetric method or the auto-diametric method (Thorsen and Kjesbu, 2001;
194 Thorsen et al. 2006). As above, only fish without any indication of having started
195 spawning were included in the fecundity analyses. Sagittal otoliths were removed
196 from each individual for stock separation (Rollefsen, 1934) since coastal cod (a
197 separate stock) also occur in the same area. Only Barents Sea cod were used in this
198 investigation. The selection programme was not completely random because the less

abundant large females were taken preferentially to ensure all length classes present in the population were represented.

2.4. Icelandic cod fecundity samples

Samples from Icelandic cod were collected each year from 1995 to 2000 in January to February, i.e., prior to the spawning season, at the main spawning grounds off the south-west coast of Iceland (Fig. 1, Marteinsdóttir and Begg, 2002). Potential fecundity estimates were determined gravimetrically from counts of oocytes in weighed portions (0.3 g) of ovary tissue as detailed in Marteinsdóttir and Begg (2002). Since oocyte diameters were not recorded for Icelandic cod, oocyte packing densities (number per gram ovary) from the gravimetric counting were converted to mean oocyte diameter using the reversed auto-diametric oocyte density versus diameter relationship (Thorsen and Kjesbu, 2001).

2.5. Calculations and statistics

Condition of fish was calculated as: 100 × whole fish weight/total fish length^3. Fecundity and fish data for all the stocks were combined into a single database and analyzed using STATA™ 10 (http://www.stata.com). Only pre-spawning fish with mean vitellogenic oocyte diameter larger than 300 µm were included in the data set. Unless otherwise noted all regression analysis were based on ln transformed data. Both simple and multiple linear regressions were used.

Potential fecundity was defined as the standing stock of vitellogenic oocytes, while relative fecundity was defined as the potential fecundity divided on total fish weight. In cases were relative fecundity was calculated from model output, fish weight was calculated from stock-specific length-weight relationships.

The standing stock of vitellogenic oocytes of cod is known to decrease as the vitellogenic oocytes grow towards start of spawning due to atresia (Thorsen et al., 2006). The fecundity samples for this study were collected over many years and at different locations. We therefore expected that differences in sampling times between years and locations might lead to skewed fecundity estimates. To standardize across stocks and years, output from the regression models utilised a constant mean oocyte diameter for each of the stocks. We chose to use 600 µm as standard value as

compromise between being close to start of spawning and to avoid extrapolation of the regression models. For calculation of cumulative fecundity the same procedure was used.

For stocks or years where oocyte diameter measurements were not available, oocyte packing densities (number per gram ovary) from gravimetric counting were converted to mean oocyte diameter using the reversed auto-diametric oocyte density versus diameter relationship (Thorsen and Kjesbu, 2001).

3. Results

3.1 Characteristics of the sampled fish

The mature female cod sampled in this investigation covered a large length range, 34 to 133 cm (Table 1). On average the Icelandic cod were the largest with a mean length of 94 cm, followed by the Barents Sea cod (82 cm). The North Sea cod were smaller (mean length, 69 cm), but still considerably larger than the Irish Sea cod (55 cm). Within each stock the difference in mean length between years was in general small with two exceptions; the Barents Sea cod sampled in 1987 were about 22 % smaller than the average for the studied period while the Irish Sea cod differed by 28 % between the two years sampled.

The average condition of the sampled cod followed a clear North-South gradient ranging from 0.89 for the Barents Sea cod to 1.27 for the Irish Sea cod. Within each stock there was considerable variation between years, but in general there was little overlap of the averages between stocks.

Mean oocyte diameter of the sampled fish was on average larger for the Barents and Irish Sea cod (644 and 672 µm) than for the Icelandic and North Sea cod (570 and 573 µm). In regard to an individual fish, spawning usually starts when the mean diameter is between 600-800 µm (Kjesbu et al., 1990; Kjesbu and Kryvi, 1993; Thorsen and Kjesbu, 2001, Thorsen et al., 2006) which in this case indicates that at sampling the Barents Sea and the Irish Sea cod were generally close to the start of spawning, while the North Sea cod and Icelandic cod were in earlier stages of development prior to spawning. There was little difference between years in mean

oocyte diameter for the Barents Sea and Irish Sea cod while for the Icelandic and North Sea cod there were large differences.

Analyses of recent time series (see Section 2.1 and 2.5 for details) on length at age showed that Barents Sea and Icelandic cod had similar growth rates (Fig. 2). North Sea and especially Irish Sea cod had considerable higher growth rates. At age three the Barents Sea cod were on average 34 cm while Icelandic cod were 39 cm. North Sea and Irish Sea cod aged 3 years, however, were on average 47 and 65 cm, respectively.

As a consequence, age at first maturity was much higher for Barents Sea and Icelandic cod than for the two other stocks (Table 2). Both the Barents Sea and Icelandic cod females matured, on average, for the first time at about 7 years old, while in North Sea and Irish Sea cod they were 4 and 2 years old, respectively. Length at first maturity (Table 2) seemed to follow a North – South gradient with first maturity at much smaller lengths in the south compared to the north.

3.2. Potential fecundity

3.2.1. Relative potential fecundity and down-regulation

The relative potential fecundity (Fig. 3) for all stocks, except the Irish Sea, decreased significantly as the mean vitellogenic oocyte diameter increased towards the start of spawning. This was also mostly the case when data were allocated to year. An explanation of the lack of decrease in relative fecundity for Irish Sea cod might be that there was a considerably narrower mean oocyte size range for the sampled fish in this area than for the other areas. Most of the Irish Sea cod appeared to have been sampled close to the start of spawning.

The data were also divided in to three different condition levels (less than 0.9, between 0.9 and 1.1, and above 1.1). For fish with condition between 0.9 and 1.1, Irish Sea cod had a reduction in relative fecundity ($P = 0.056$, $r^2 = 0.55$), although the small number of observations ($n = 6$) in this condition interval did not allow firm conclusions to be made. The reduction in relative fecundity for the other cod stocks did not seem to be influenced by condition.

Because the potential fecundity generally decreased as the mean oocyte diameter increased, i.e., as spawning time became closer, we included mean oocyte diameter as one of the independent variables in our fecundity regression models.

3.2.2. Potential fecundity regressions

Potential fecundity regressions were made for all stocks and sampling years (Table 3). All regressions were highly significant ($P < 0.001$). Length was used as an independent variable either alone or in combination with mean oocyte diameter and/or condition. When length alone was used as an independent variable r^2 varied between years from 0.75 to 0.92 and there appeared to be only small differences between the stocks. When mean oocyte diameter was included as an additional independent variable, r^2 in all cases increased, typically between 0.01 and 0.03. However, for Irish Sea cod this was less and insignificant ($P > 0.05$). When condition was also added as one of the independent variables there was a greater increase in r^2, typically 0.03 to 0.04, resulting in r^2 for several cases being above 0.94.

3.2.3. Potential fecundity from year independent regression models

When calculating potential fecundity (Fig. 4) from the year independent models there were only minor differences in output when using only length (Fig. 4 A) or including mean oocyte diameter (Fig. 4 B) as an additional independent variable. For calculating the output from models including mean oocyte diameter, a diameter of 600 µm was used as the normalised setting for all cases. This number was not very far from the actual overall averages for each of the stocks (Table 1), which explains the small differences between the two model types. In general the models showed that there was a north-south difference with considerably higher fecundity in the south. This difference was slightly larger for large fish than for small fish; using the model with length and oocyte diameter as independent variables (Fig. 4 B) a 60-cm cod from the Irish Sea was about 2.5 times more fecund than a 60-cm cod from the Barents Sea, but this factor increased to about 2.8 for 90-cm fish. Using the models including length and oocyte diameter (Fig. 4 B) a 60-cm fish from Icelandic waters was slightly less fecund than a similar sized fish from the Barents Sea (0.76 versus 0.64 million oocytes) while this was the opposite for a 90-cm fish (3.30 versus 4.05 million). The model output indicated that North Sea cod was considerably more fecund than the two

334 northerly stocks while the Irish Sea cod was even higher. A 60-cm Irish Sea cod was
335 27 % more fecund than a similar North Sea cod while a 90-cm fish was predicted to
336 be 49 % more fecund.
337
338 Comparing relative fecundity (Table 4, see section 2.5 for how relative fecundity was
339 calculated) for the different stocks revealed that the Barents Sea and Icelandic stocks
340 were similar for small fish, but Icelandic cod seemed to become disproportionally
341 more fecund as their body mass increased. North Sea cod was considerable more
342 fecund than the two northerly stocks while Irish Sea cod was even higher.
343
344 We also calculated fecundity for 60 and 90 cm fish from the models that included
345 both length, mean oocyte diameter and condition as independent variables (Fig. 4 C),
346 again mean oocyte diameter was set to 600 µm, while 1.1 was chosen as a standard
347 condition factor value. This value was chosen since the stocks at this point had
348 overlap in condition even though their mean condition levels were different (Table 1).
349 Comparing output from this model revealed smaller differences between the stocks
350 (Fig. 4 C). Barents Sea cod and Icelandic cod had a similar level of fecundity, while
351 the North Sea and Irish Sea cod fecundities were still about 30-50 % higher than the
352 more northerly stocks. When comparing North Sea and Irish Sea cod, a 60-cm fish
353 from the two stocks was almost equally fecund, while for a 90-cm fish the Irish Sea
354 cod was still about 17 % more fecund.
355
356 3.2.4. Year effects on potential fecundity
357 For Barents Sea and Icelandic cod stocks, yearly variations in fecundity over the 10
358 and 6 years time series were examined (Figs. 5 and 6). In both cases we chose to
359 compare a 80-cm fish since this size was represented in all years in both stocks (Table
360 1) and also could be considered as a typical size of spawning fish. For Barents Sea
361 cod (Fig. 5) there was little difference between the output from the models with
362 length or length and mean oocyte diameter as independent variables. This was
363 probably because for this stock there was little difference between the overall mean
364 oocyte diameters for the sampled material (Table 1) and the standard setting of 600
365 µm that we used for input in the models that included mean oocyte diameter.
366 For the Icelandic cod however, there were larger differences in the sampled mean
367 oocyte diameter (Table 1). Therefore, in this case including diameter in the model

changed the output considerably (Fig. 6). Except for 1998 the years were very similar with a maximum of 10 % difference. However, between 1998 and the other years the difference increased since the sampled fish were much less developed, i.e., farther away from initiating spawning, than in the other years. In 1998 the mean oocyte diameter was only 493 µm. In the length based model there was a maximum of 42 % difference in fecundity between the highest (1999) and the lowest (1998) year while this increased to 51 % (compared to 1996) when mean oocyte diameter was included. A closer examination of the 1998 data showed that the reduction in relative fecundity by increasing diameter was highly significant ($P \leq 0.000$, $r^2 = 0.22$, $n = 92$) and that the whole range of diameters from 400-600 µm was well represented in the data. Thus the large reduction in predicted fecundity that we calculated for Icelandic cod in 1998 seemed justified.

Comparing the output from the model (Fig. 5) with length and mean oocyte diameter the Barents Sea cod had less difference between the high and low fecundity years than did the Icelandic cod (Fig. 6). For the Barents Sea cod the most fecund year was 2003 and the less fecund year was 1987, which was 37 % lower (from model including length and mean oocyte diameter).

In an attempt to reveal how condition affected potential fecundity condition was added as an independent variable in the regression models that already included length and mean oocyte diameter (Figs. 5 and 6). Here we used the average condition of fish in the stock for all years as an input. If condition was the major driving force for the observed yearly differences in fecundity using an overall average as input should remove most of these differences. For Barents Sea cod using the grand average condition factor of 0.89 made the different years in general more similar (Fig. 5). For the Icelandic cod the average condition of fish in the stock was 1.06. Using this as an input for the Icelandic cod altered the output, but less than for Barents Sea cod, and the differences between years were similar to previous models including length and diameter (Fig. 6). The larger effect of condition we saw on the Barents Sea cod fecundity can probably be explained by the larger variation in condition between years that exist for this stock. For the Barents Sea cod the yearly averages varied between 0.73 and 0.95, a 30 % difference, while the Icelandic cod only varied between 1.00 and 1.13, a difference of 13 %.

The stocks on average spawn for the first time at different age and size (Table 2) and have different growth rates (Fig. 2) and condition (Table 1). To see how the egg production compared over time we calculated cumulative fecundity by age and number of spawning periods (Fig. 7). Doing this we could clearly see that the Irish Sea cod produced far fewer eggs during the first spawning period than did the other stocks. While the Irish Sea cod only produced about 0.3 million eggs during the first spawning period the other stocks produced from 1.7 - 2.2 million eggs. However, since the Irish Sea cod started at much younger age they produced many more eggs than did the other stocks at the following ages. At an age of 5 when the Irish Sea cod had finished 4 spawning periods and produced 14 million eggs the Barents Sea cod and Icelandic cod had not even started to spawn. After 4 spawning periods the number of spawned eggs were rather similar for all the stocks except for the North Sea cod that seemed to produce about 40 % more than the others.

4. Discussion

This study demonstrated large differences in egg production among Atlantic cod distributed over a wide latitudinal and temporal range. Cod from southerly located stocks were shown to be substantially more fecund that those residing at northerly located latitudes.

Growth rate is generally considered to be a key factor that influences age at first maturity (Karlsen et al., 2006; Kuparinen et al., 2008; Olsen et al., 2009; Svåsand et al., 1996;Taranger et al., 2009;) and is strongly dependent on temperature in combination with food intake. The difference in temperature regime from the Barents Sea in the north to the Irish Sea in the south can be considered to represent the full thermal range for cod (Sundby, 2000). These differences in temperature is probably a major driving force for the differences that we see in growth rate, age at first maturity and maybe also fecundity (Kjesbu et al., 2010) for the four cod stocks. However, we also see a gradient from north to south in prespawning condition, with much higher conditions in the south. To attain the very high condition factors found in the south, food availability may be higher and for longer during the year. In addition the more southern stocks do not undertake such long migrations thus there are less alternate energetic demands on calorie intakes. The cod stocks in the south have been severely

436 reduced during the last decades by high fishing pressure (Brunel and Boucher, 2007;
437 Kell et al., 2006), - although changes in environment and recruitment failure may also
438 have contributed to the situation. The low abundance of cod in the south possibly
439 reduces competition for food with increased growth rates and condition as results.
440 However, high fishing mortality may also favour fish that genetically has a tendency
441 for early maturation (Jørgensen et al., 2008). Thus, high fishing pressure may cause
442 both phenotypic responses causing rapid growth and early maturation as well as
443 genetic drift over time pushing in the same direction. Even for Barents Sea cod, which
444 is regarded to be in a fairly good state, the age and size at first maturity seems to have
445 been reduced during the last decades compared to the post-war situation (Nash et al.,
446 this issue). For North Sea cod the situation is less clear. Females during the period
447 from 1981-2001 on average matured at a length of 62 cm (Table 2), but with very
448 large variation from 40-77 cm (Nash et al., this issue). Older reports by Graham
449 (1924) and Holt (1883) both suggested an average maturation length of 74 cm. Stock
450 depletion may, however, not be the only reason for today's situations, since in the last
451 two decades there has been a rise in temperature both in the North Sea (Dulvy et al.,
452 2008; Skogen et al., 2009) and the Barents Sea (Ingvaldsen, 2009).
453
454 Barents Sea cod and Icelandic cod apparently experience similar temperature regimes
455 (Sundby, 2000) and although our data suggests Icelandic cod are slightly more fecund
456 than the Barents Sea cod they are basically relatively similar. The slightly lower
457 fecundity of the Barents Sea cod might be explained by the very long spawning
458 migration of this cod. The North Sea cod and the Irish Sea cod on the other hand
459 experience higher temperatures, especially the Irish Sea cod. These cod stocks also
460 seem to have considerably higher fecundities, especially the Irish Sea cod which has a
461 relative fecundity far above the other cod stocks. The elevated fecundities at higher
462 temperatures are in agreement with laboratory studies of Kjesbu et al. (2010).
463
464 A 90-cm Irish Sea cod in our investigation had a predicted relative potential fecundity
465 about 80 % higher than a Barents Sea cod (Table 4). Also this type of fecundity
466 estimate was considerable higher than for the other cod stocks. However, when
467 comparing fecundity at the first and second spawning the Irish Sea cod had
468 considerable lower fecundity than the other stocks. Due to a high mortality we can
469 probably consider that spawning more than twice is rare for some of the cod stocks in

question (Ottersen, 2008). At any age expected fecundity of Irish Sea cod is far higher than the other stocks, but since they start production at such low age and size our estimations indicate a low production during their expected reproductive life (Fig. 7). This may indicate that high mortality of cod in the Irish Sea is a dominant factor that favours individuals with an extremely early start of egg production, both in terms of age and size. However, experiments with Barents Sea cod in tanks (Svåsand et al., 1996) also suggest that at a large part of the reason for this is a direct physiological response to high temperature and growth. Barents Sea cod females in aquaculture have been reported to mature at an age of 2 years and at an average length of 45 cm (Svåsand et al., 1996).

Both for Barents Sea cod and Icelandic cod we found considerable variation in fecundity between years. Adding condition factor to the multiple regression models helped reveal whether these differences were caused by yearly differences in prespawning condition. Our results indicated that prespawning condition could only partly explain the yearly differences in fecundity. Skjæraasen et al. (2006) found in tank experiments that female cod energy reserves at the onset of vitellogenesis 3-4 months before spawning had the highest explanatory power for potential fecundity. Possible the recruitment of oocytes into vitellogenesis is strongly influenced by the condition at onset of vitellogenesis, while condition closer to spawning or during spawning determines the level of atresia that reduced the standing stock of maturing oocytes to the numbers that were actually going to be spawned. In our investigation it was the prespawning condition that was used. If the condition at start of vitellogenesis had been used instead, or in addition, the explanatory power of condition might have been higher, although it has been recently shown that temperature influences the timing of this peak production of oocytes (Kjesbu et al., 2010).

Determinate spawners are often classified as capital breeders and reproductive investment is heavily dependent on the feeding season prior to the major yolk production that take place during vitellogenesis (Boulcott and Wright, 2008). A typical example of such is the Norwegian spring-spawning herring that incorporate the majority of yolk into the oocytes after the feeding season has ended in early autumn (Kurita et al., 2003), and then spawn in the following spring without significant feeding in between (Dommasnes et al., 2004). Cod do not, in general, seem to have such an extreme strategy, feeding is common also during late vitellogenesis

and may also take place during parts of the spawning cycle (Dolgov, 2002; Michalsen et al., 2008). Therefore fecundity of cod is probably influenced both by condition at the onset of vitellogenesis (Skjæraasen et al., 2009) and condition during subsequent oocyte maturation and spawning. Most likely, the condition at the onset of vitellogenesis is determinate for the number of oocytes that will start vitellogenesis while feeding and condition later during maturation influence final fecundity by atresia.

The timing of sampling over these time series varied with respect to the proximity to the spawning season of the stock in question. Since atresia can significantly reduce the standing stock of maturing oocytes as spawning approaches such differences can bias fecundity estimations considerably (Kennedy et al., 2007; Kurita et al., 2003; Thorsen et al., 2006; Witthames et al., 2009). Following the recommendations given by Thorsen et al. (2006), we have included mean oocyte diameter, using as a proxy for maturity, as one of the independent variables in the fecundity regressions to account for the loss of fecundity prior to spawning. The objective was to minimise any effects of the maturity schedule (annual timing of development) on the fecundity estimations and standardize the estimations of fecundity to prespawning levels. In our investigation this mostly made a difference in the comparisons between years and very little when comparing stocks. The explanation for this can be found when comparing mean oocyte diameters (Table 1); grand averages for the four stocks showed only minor differences while within stock comparisons in some cases revealed differences that had considerable influence on the yearly estimates. This was especially the case for Icelandic cod.

The use of mean oocyte diameter as a proxy for maturation has the advantage for time series such as those dealt with here because it can be calculated from the number of oocytes per gram ovary (Thorsen et al., 2006). Both individual ovary weight and fecundity are usually available in the fecundity data sets since it is the basis for the calculation of potential fecundity. However, for determinate batch spawners, such as cod, the leading cohort diameter (mean of the largest 10% of advanced oocytes in the ovary) may be a better proxy for maturation because of its close link and sensitivity to the start of spawning (Kjesbu, 1994; Kjesbu et al., 2010). In pilot tests we have found that leading cohort can be used instead of mean oocyte diameter in our present

models. We have not used this information here because it is only available for some of the stocks and only in the most recent observations where fecundity was determined by image analysis (Thorsen and Kjesbu, 2001).

Using mean oocyte diameter to standardize to pre-spawning fecundity can be considered as a way of accounting for pre-spawning atresia without the laborious estimation of atresia levels. The alternative is to measure the standing stock of atresia throughout maturation, by histology, and then estimate the reduction of the standing stock of maturing oocytes (Andersen, 2003; Hunter and Macewicz, 1985; Hunter et al., 1992; Kurita et al., 2003; Murua et al., 2003). However, to make this adjustment it is also necessary to know the duration of the counted atretic stage (usually the alpha-stage) and the time until start of spawning (Murua et al., 2003). The duration of the atretic stage is seldom accurately known (Witthames et al., this issue) and is generally difficult to estimate. To estimate realised fecundity it is also necessary to estimate the atretic loss during the spawning period which is even further complicated since, during this period, oocytes are lost both by spawning events and atresia. Whilst we are aware of this and research is being undertaken, further research is still necessary before quantitative relationships can be included.

In our between year fecundity comparisons, Icelandic cod in 1998 stood out as exceptionally low fecundity compared to the other stocks and years. However, this was only apparent when mean oocyte diameter was introduced into the regression and oocyte diameter was standardised to a prespawning level (600 µm). Without this standardisation the fecundity of 1998 was still low, but only slightly lower than for 1995 and 1997. We consider that the explanation of fecundity loss observed during the maturation process is consequential to the production of atretic follicles from normal developing oocytes. This view is further supported by Kjesbu et al. (this issue) and from earlier work (Kurita et al., 2003; Thorsen et al., 2006; Witthames et al., 2009) including other determinate species such as sole (*Sole solea*) (Witthames and Greer Walker, 1995). An alternative explanation to this however, is that this is a trade-off between size and number of spawned eggs. There are two reasons why we do not think this is an important factor. First, the sharpest reduction in relative fecundity seems to occur during early vitellogenesis (300-500 µm) which is well before the oocytes are ready to start final maturation. Typically the oocytes have a mean

diameter of 600-800 µm just prior to final maturation (Table 1). A second argument against the size versus number trade-off is that much of the spawned egg size adjustment actually seems to happen during final maturation that take place the last 2-3 days before release of each batch (Kjesbu et al., 1996). During this phase the uptake rate of vitellogenin may be extraordinary large (Wallace and Selman, 1985).

In summary, we conclude that both size and age of sexual maturity, growth and fecundity of cod in the North Eastern part of the Atlantic is extremely variable with clear gradients from North to South. Cod in cold waters have low growth rate and fecundity and also mature later in life. Cod in warmer water have much higher growth rates and fecundity but mature at a very early age. The major driving force for these differences are probably temperature, but fishing pressure and food availability most probably also contribute.

Acknowledgements

This work was supported by the EU (RASER- Q5RS-2002-01825). The production of this article was encouraged by discussions with and the terms of reference of the NAFO Working Group on Reproductive Potential and COST Action Fish Reproduction and Fisheries (FRESH, FA0601).

References

Andersen, T.E., 2003. Unbiased stereological estimation of cell numbers and volume fractions: the disector and the principles of point counting. In: Modern Approaches to Assess Maturity and Fecundity of Warm- and Cold-Water Fish and Squids (Kjesbu O.S, Hunter, J.S., and Witthames P.R. eds.), Fisk. Hav. 12, 11-18.

Armstrong, M.J., Connolly, P., Nash, R.D.M., Pawson, M.G., Alesworth, E., Coulahan, P.J., Dickey-Collas, M., Milligan, S.P., O'Neill, M.F., Witthames, P.R., Woolner, L., 2001. An application of the annual egg production method to estimate the spawning biomass of cod (*Gadus morhua* L.), plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) in the Irish Sea. ICES J. Mar. Sci. 58, 183-203.

Bergstad, O., Jørgensen, T., Dragesund, O., 1987. Life-history and ecology of the

607 gadoid resources of the Barents Sea. Fish. Res. 5, 119-161.
608 Beverton, R.J.H., Holt, S.J., 1957. On the dynamics of exploited fish populations.
609 U.K. Min. Agric. Fish, Fish. Invest. (Ser. 2) 19., 1-533.
610 Boulcott, P., Wright, P., 2008. Critical timing for reproductive allocation in a capital
611 breeder: evidence from sandeels. Aquat. Biol. 3, 31-40.
612 Brunel, T., Boucher, J., 2007. Long-term trends in fish recruitment in the north-east
613 Atlantic related to climate change. Fish. Oceanogr. 16, 336-349.
614 Dolgov, A.V., 2002. The role of capelin (*Mallotus villosus*) in the foodweb of the
615 Barents Sea. ICES J. Mar. Sci. 59, 1034-1045.
616 Dommasnes, A., Melle, W., Dalpadado, P., Ellertsen, B., 2004. Herring as a major
617 consumer in the Norwegian Sea. ICES J. Mar. Sci., 61, 739-751.
618 Dulvy, N., Rogers, S., Jennings, S., Stelzenmuller, V., Dye, S., Skjoldal, H., 2008.
619 Climate change and deepening of the North Sea fish assemblage: a biotic
620 indicator of warming seas. J. Appl. Ecol. 45, 1029-1039.
621 Fulton, T.W., 1898. On the growth and maturation of the ovarian eggs of teleostean
622 fishes. Sixteenth Annual Report of the Fishery Board for Scotland
623 Graham, M., 1924. The annual cycle in the life of the mature cod in the North Sea.
624 Fish. Invest., Lond. (2). 6, 1-77.
625 Greer Walker, M., Witthames, P.R., De Los Santos, I.B., 1994. Is the fecundity of the
626 Atlantic mackerel (*Scomber scombrus*: Scombridae) determinate? Sarsia 79,
627 13-26.
628 Harden-Jones F. R. 1968. Fish Migration. Edward Arnold London.
629 Holt, E.W.L., 1893. North Sea investigations. J. Mar. Biol. Ass. U.K. 3, 78-122.
630 Hunter, J.R., Macewicz, B.J., 1985. Rates of atresia in the ovary of captive and wild
631 northern anchovy, *Engraulis-Mordax*. Fish. Bull. US 83, 119-136.
632 Hunter, J.R., Macewicz, B.J., Lo, N.C.-H., Kimbrell, C.A., 1992. Fecundity,
633 spawning, and maturity of female Dover sole *Microstomus pacificus*, with an
634 evaluation of assumptions and precision. Fish. Bull, US 90, 101-128.
635 ICES. 2005. Spawning and life history information for North Atlantic cod stocks.
636 ICES Coop. Res. Rep. 274. 152 pp.
637 Ingvaldsen, R., 2009. 1.2.1 Fysikk (sirkulasjon, vannmasser og klima), Havets
638 ressurser og miljø. Fisk. Hav. 1, 25-27.

639 Jonsdottir, I., Marteinsdóttir, G., Campana, S., 2007. Contribution of different
640 spawning components to the mixed stock fishery for cod in Icelandic waters.
641 ICES J. Mar. Sci. 64, 1749-1759.
642 Jørgensen, C., Dunlop, E., Opdal, A., Fiksen, O., 2008. The evolution of spawning
643 migrations: state dependence and fishing-induced changes. Ecology 89, 3436-
644 3448.
645 Karlsen, O., Norberg, B., Kjesbu, O., Taranger, G., 2006. Effects of photoperiod and
646 exercise on growth, liver size, and age at puberty in farmed Atlantic cod
647 (*Gadus morhua* L.). ICES J. Mar. Sci. 63, 355-364.
648 Kelly, C., Codling, E., Rogan, E., 2006. The Irish Sea cod recovery plan: some
649 lessons learned. ICES J. Mar. Sci. 63, 600-610.
650 Kennedy, J., Witthames, P.R., Nash, R.D.M, 2007. The concept of fecundity
651 regulation in plaice (*Pleuronectes platessa*) tested on three Irish Sea spawning
652 populations. Can. J. Fish. Aquat. Sci. 64, 587-601.
653 Kjesbu, O.S., 1994. Time of start of spawning in atlantic cod (*Gadus morhua*) females
654 in relation to vitellogenic oocyte diameter, temperature, fish length and
655 condition. J. Fish Biol. 45, 719-735.
656 Kjesbu, O.S., Kryvi, H., 1993. A histological examination of oocyte final maturation
657 in cod (*Gadus morhua* L.). In: Physiological and Biochemical Aspects of Fish
658 Development. (Walter, B. T. & Fyhn, H. J., eds.), 86-93.
659 Kjesbu, O.S., Witthames, P.R., Solemdal, P., Greer Walker, M., 1990. Ovulatory
660 rhythm and a method to determinate the stage of spawning in Atlantic cod
661 (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 47, 1185-1193.
662 Kjesbu, O.S., Kryvi, H., Norberg, B., 1996. Oocyte size and structure in relation to
663 blood plasma steroid hormones in individually monitored, spawning Atlantic
664 cod. J. Fish Biol. 49, 1197-1215.
665 Kjesbu, O.S., Witthames, P.R., Solemdal, P., Greer Walker, M., 1998. Temporal
666 variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in
667 response to natural changes in food and temperature. J. Sea Res. 40, 303-321.
668 Kjesbu, O.S., Fonn, M., Gonzáles, B.D., Nilsen, T., 2010. Stereological calibration of
669 the profile method to quickly estimate atresia levels in fish. Fish. Res., this
670 issue.

671 Kjesbu O.S., Righton, D., Krüger-Johnsen, M., Thorsen, A., Michalsen, K., Fonn, M,
672 Witthames, P.R., 2010. Thermal dynamics of ovarian maturation in Atlantic
673 cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 67, 605-625.
674 Kuparinen, A., O'Hara, R.B., Merilae, J., 2008. The role of growth history in
675 determining age and size at maturation in exploited fish populations. Fish Fish.
676 9, 201-207.
677 Kurita, Y., Meier, S., Kjesbu, O., 2003. Oocyte growth and fecundity regulation by
678 atresia of Atlantic herring (*Clupea harengus*) in relation to body condition
679 throughout the maturation cycle. J. Sea Res. 49, 203-219.
680 Ma, Y., Kjesbu, O.S., Jørgensen, T., 1998. Effects of ration on the maturation and
681 fecundity in captive Atlantic herring (*Clupea harengus*). Can. J. Fish. Aquat.
682 Sci. 55, 900-908.
683 Marteinsdóttir, G., Begg, G., 2002. Essential relationships incorporating the influence
684 of age, size and condition on variables required for estimation of reproductive
685 potential in Atlantic cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 235, 235-256.
686 Michalsen, K., Johannesen, E., Bogstad, L., 2008. Feeding of mature cod (*Gadus*
687 *morhua*) on the spawning grounds in Lofoten. ICES J. Mar. Sci. 65, 571-580.
688 Milroy, T.H., 1898. The physical and chemical changes taking place in the ova of
689 certain marine teleosteans during maturation. Sixteenth Annual Report of the
690 Fishery Board for Scotland 135-152.
691 Murua, H., Kraus, G., Saborido-Rey, F., Witthames, P., Thorsen, A., Junquera, S.,
692 2003. Procedures to estimate fecundity of marine fish species in relation to
693 their reproductive strategy. J. Northw. Atl. Fish. Sci. 33, 33-54.
694 Nash, R.D.M., Pilling, G.M., Kell, L.T., Schön, P-J., Kjesbu, O.S. 2010. Investment
695 in maturity at age and length in northeast Atlantic cod stocks. Fish. Res., this
696 issue.
697 Olsen, E.M., Carlson, S., Gjøsæter, J., Stenseth, N., 2009. Nine decades of decreasing
698 phenotypic variability in Atlantic cod. Ecol. Lett. 12 (7), 622-631.
699 Óskarsson, G. J., Kjesbu, O.S., Slotte, A., 2002. Predictions of realised fecundity and
700 spawning time in Norwegian spring-spawning herring (*Clupea harengus*). J.
701 Sea Res. 48, 59-79.
702 Ottersen, G., 2008. Pronounced long-term juvenation in the spawning stock of Arcto-
703 Norwegian cod (*Gadus morhua*) and possible consequences for recruitment.
704 Can. J. Fish. Aquat. Sci. 65, 523-534.

Righton, D., Quayle, V., Hetherington, S., Burt, G., 2007. Movements and distribution of cod (*Gadus morhua*) in the southern North Sea and English Channel: results from conventional and electronic tagging experiments. J. Mar. Biol. Assoc. Uk. 87, 599-613.

Robichaud, D., Rose, G., 2004. Migratory behaviour and range in Atlantic cod: inference from a century of tagging. Fish Fish. 5, 185-214.

Roff, D. A. 2000. Trade-offs between growth and reproduction: an analysis of the quantitative genetic evidence. J.Evol. Biol. 434-445.

Rollefsen, G., 1934. The cod otolith as a guide to race, sexual development and mortality. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 88, 1-5.

Rowell, C.A., 1993. The effects of fishing on the timing of maturity in North Sea cod (*Gadus morhua* L.). Lect Notes Biomath. 99, 44–61

Schopka, S. A. 1993. The Greenland cod (*Gadus morhua*) at Iceland 1941–90 and their impact on assessments. NAFO Sci. Coun. Studies, 18, 81–85

Skogen, M.D., Danielssen, D., Hjøllo, S., Søiland, H., 2009. Fysikk (sirkulasjon, vannmasser, klima, næringssalter og oksygen), Havets ressurser og miljø. Fisk. Hav. 1, 102-105.

Skjæraasen, J.E., Kennedy, J., Thorsen, A., Fonn, M., Strand, B.N., Mayer, I., Kjesbu, O.S., 2009. Mechanisms regulating oocyte recruitment and skipped spawning in Northeast Arctic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 66, 1582-1596.

Skjæraasen, J.E., Nilsen, T., Kjesbu, O.S., 2006. Timing and determination of potential fecundity in Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 63(2), 310-320.

Smith C. C. and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. Amer. Natur. 108, 499

Stearns S.C., 1992. The Evolution of Life Histories. Oxford University Press, Oxford

Stearns, S.C., 2000. Life history evolution: successes, limitations, and prospects. Naturwissenschaften. 87, 476-486.

Sundby, S., 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. Sarsia 85, 277-298.

Sundby, S., Nakken, O., 2008. Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. ICES J. Mar. Sci. 65: 953–962.

739 Svåsand, T., Jørstad, K.E., Otterå, H., Kjesbu, O.S., 1996. Differences in growth
740 performance between Arcto-Norwegian and Norwegian coastal cod reared
741 under identical conditions. J. Fish Biol. 49, 108-119.
742 Taranger G.L., C.M., Schulz R.W., Fontaine P., Zanuy S., Felip A., Weltzien F.A.,
743 Dufour S., Karlsen Ø., Norberg B., Andersson E., Hansen T., 2009. Control of
744 puberty in farmed fish. Gen. Comp. Endocr. 165, 483-515
745 Thorsen, A., and Fyhn, H.J., 1996. Final oocyte maturation *in vivo* and *in vitro* in
746 marine fishes with pelagic eggs; Yolk protein hydrolysis and free amino acid
747 content. J. Fish Biol. 48, 1195-1209.
748 Thorsen, A., Kjesbu, O., Fyhn, H., and Solemdal, P., 1996. Physiological mechanisms
749 of buoyancy in eggs from brackish water cod. J. Fish Biol. 48, 457-477.
750 Thorsen, A., Kjesbu, O., 2001. A rapid method for estimation of oocyte size and
751 potential fecundity in Atlantic cod using a computer-aided particle analysis
752 system. J. Sea Res. 46, 295-308.
753 Thorsen, A., Marshall, C.T., Kjesbu, O.S., 2006. Comparison of various potential
754 fecundity models for north-east Arctic cod *Gadus morhua*, L. using oocyte
755 diameter as a standardizing factor. J. Fish Biol. 69, 1709-1730.
756 Wallace, R.A., Selman, K., 1985. Major protein changes during vitellogenesis and
757 maturation of *Fundulus* oocytes. Devel. Biol. 110, 492-498.
758 Witthames, P.R., Greer Walker, M., 1995. Determinacy of fecundity and oocyte
759 atresia in sole (*Solea solea*) from the Channel, the North Sea and the Irish Sea.
760 Aquat. Liv. Resour. 8, 91-109.
761 Witthames, P.R., Andersson, E., Greenwood, L.N., Lyons, B., Fonn, M., Kjesbu,
762 O.S., 2003. Apoptosis in regressing follicles from *Solea solea* and *Gadus*
763 *morhua*. Fish Physiol. Biochem. 28, 377-378.Witthames, P.R., Thorsen, A.,
764 Murua, H., Saborido-Rey, F., Greenwood, L., Dominguez, R., Korta, M.,
765 Kjesbu, O.S., 2009. Advances in methods for determining fecundity:
766 application of the new methods to some marine fishes. Fish. Bull., US 107,
767 148-164.
768 Witthames, P., Thorsen, A., Kjesbu, O.S. The fate of vitellogenic follicles in
769 experimentally monitored Atlantic cod *Gadus morhua* (L.): application to
770 stock assessment. Fish. Res., this issue.
771 Wootton, R.J., 1998. Ecology of Teleost Fishes. (2nd ed.), 386.

Wright, P.J., and Trippel, E.A., 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. Fish. Fish. 10, 283-304.

Yoneda, M., Wright, P., 2004. Temporal and spatial variation in reproductive investment of Atlantic cod *Gadus morhua* in the northern North Sea and Scottish west coast. Mar. Ecol. Prog. Ser. 276, 237-248.

FIGURE LEGENDS

Fig. 1. Sampling, spawning, and distribution areas for the four studied cod stocks. Isolines show yearly mean temperature at 100 m depth. Redrawn from Sundby (2000).

Fig. 2. Growth in length for female cod in the Barents Sea, Icelandic waters, North Sea and Irish Sea based on recent time series.

Fig. 3. Relative potential fecundity (number of oocytes/total fish weight) versus mean oocyte diameter for Barents Sea cod, Icelandic cod, North Sea cod, and Irish Sea cod.

Fig. 4. Estimated potential fecundity for 60- and 90-cm cod from regression models using length (A), length and mean oocyte diameter (B), or length, mean oocyte diameter, and condition as independents (C). For calculating output from the models a mean oocyte diameter of 600 µm and a condition of 1.1 was used. Models included data for all observed years.

Fig. 5. Annual variations in fecundity of Barents Sea cod using different models. Inputs: Length = 80 cm, mean oocyte diameter = 600 µm, condition = 0.89 (grand average for Barents Sea cod).

Fig. 6. Annual variations in fecundity of Icelandic cod using different models and split on years. Inputs: Length = 80 cm, mean oocyte diameter = 600 µm, condition = 1.06 (overall average for Icelandic cod).

Fig. 7. Model output on cumulative potential fecundity by age. Each marker illustrates a spawning period. The potential fecundity was calculated from models including length, mean oocyte diameter and condition. Inputs: mean oocyte diameter = 600 µm; condition = grand average for stock (Table 1); length = L_{50} (Table 2) for first spawning period, mean length at age (Fig. 2) for later spawning periods.

Figure 1

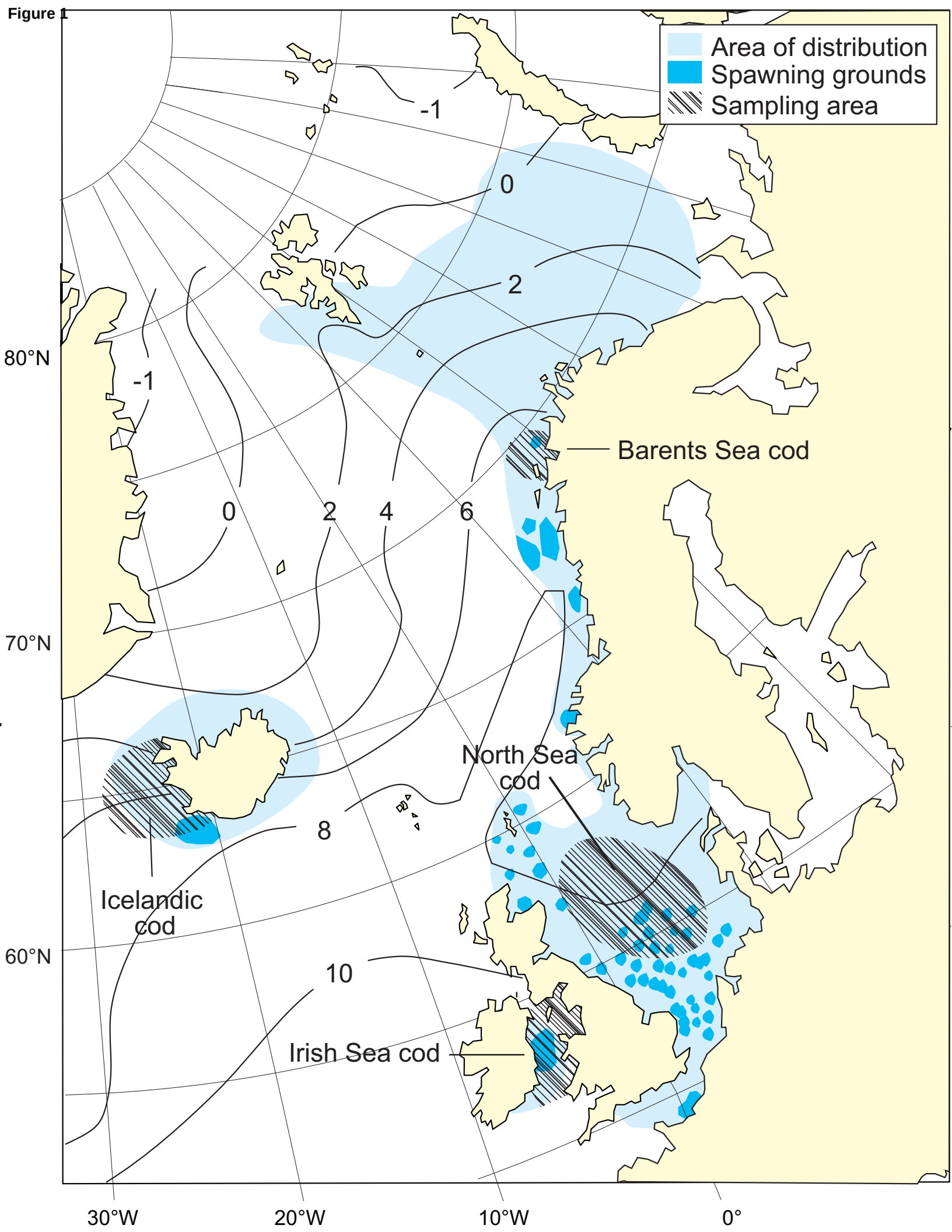
Area of distribution
Spawning grounds
Sampling area
-1
0
2
-1
0
2
4
6
8
10
Barents Sea cod
North Sea cod
Icelandic cod
Irish Sea cod
80°N
70°N
60°N
30°W
20°W
10°W
0°

Figure 2

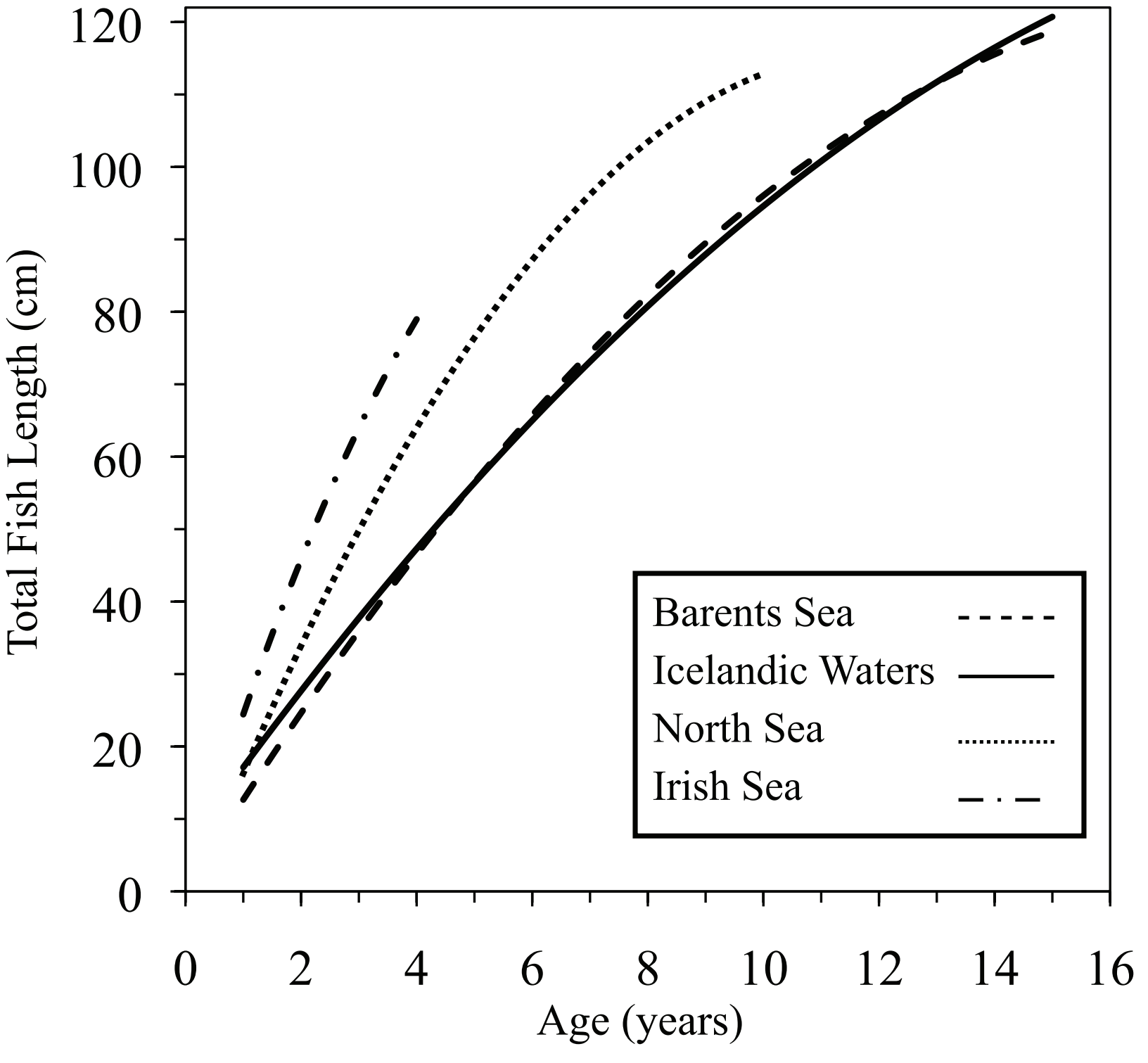
120
100
80
60
40
20
0
Total Fish Length (cm)
0
2
4
6
8
10
12
14
16
Age (years)
Barents Sea
Icelandic Waters
North Sea
Irish Sea

Figure 3

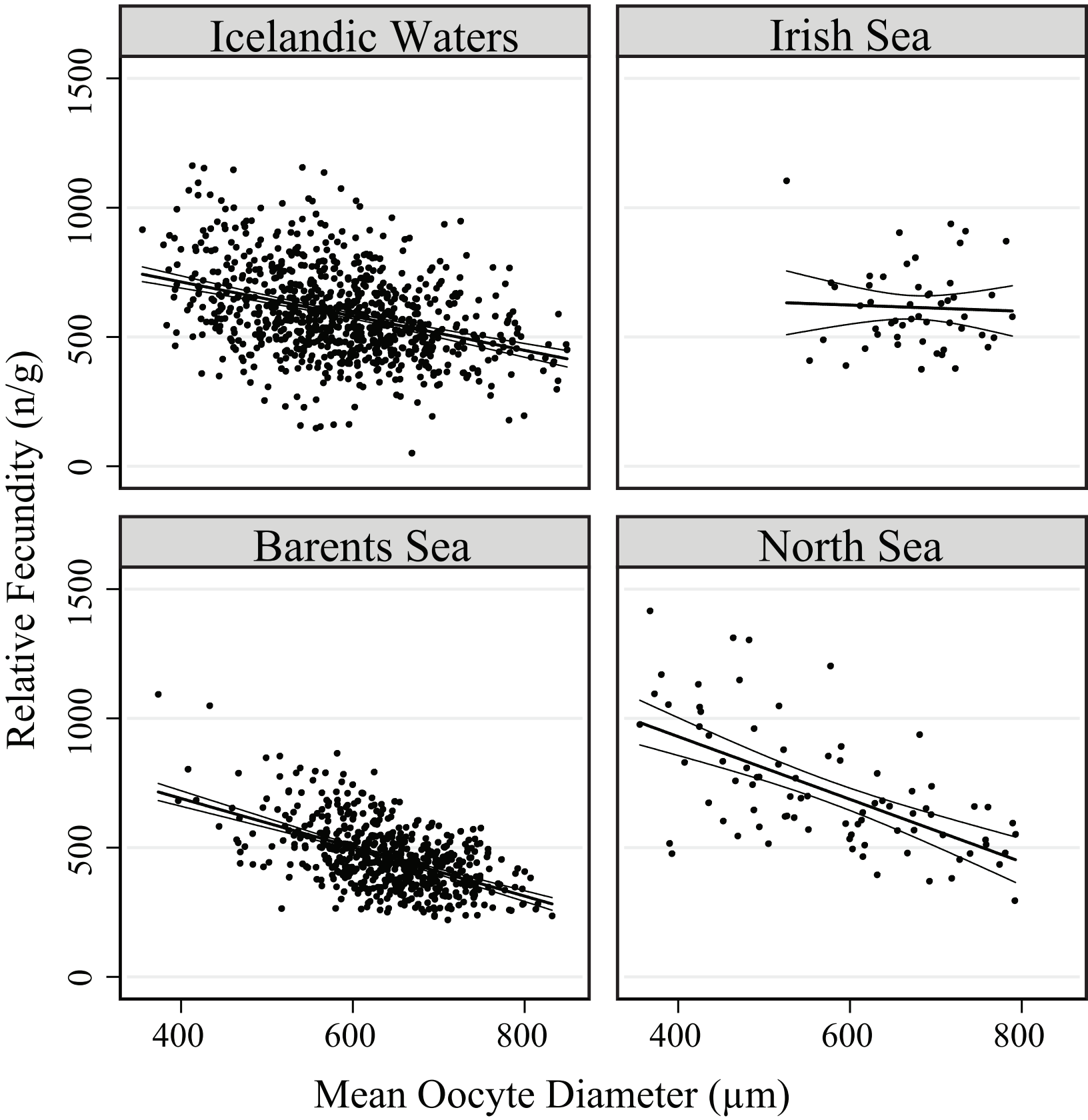
Icelandic Waters
Irish Sea
Barents Sea
North Sea
Relative Fecundity (n/g)
0
500
1000
1500
400
600
800
Mean Oocyte Diameter (µm)

Figure 4

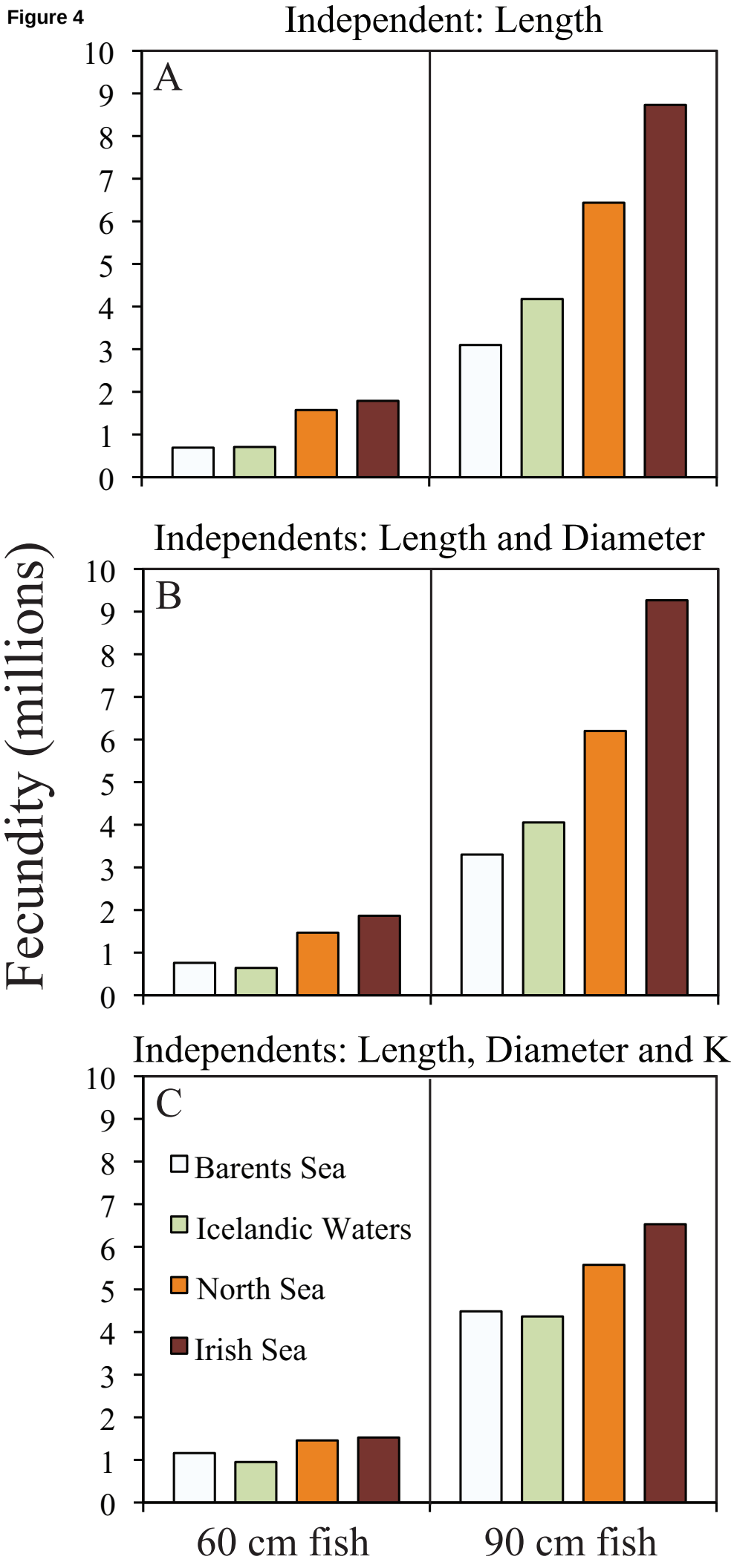
Independent: Length
A
Independents: Length and Diameter
B
Independents: Length, Diameter and K
C
Fecundity (millions)
0
1
2
3
4
5
6
7
8
9
10
Barents Sea
Icelandic Waters
North Sea
Irish Sea
60 cm fish
90 cm fish

Figure 5

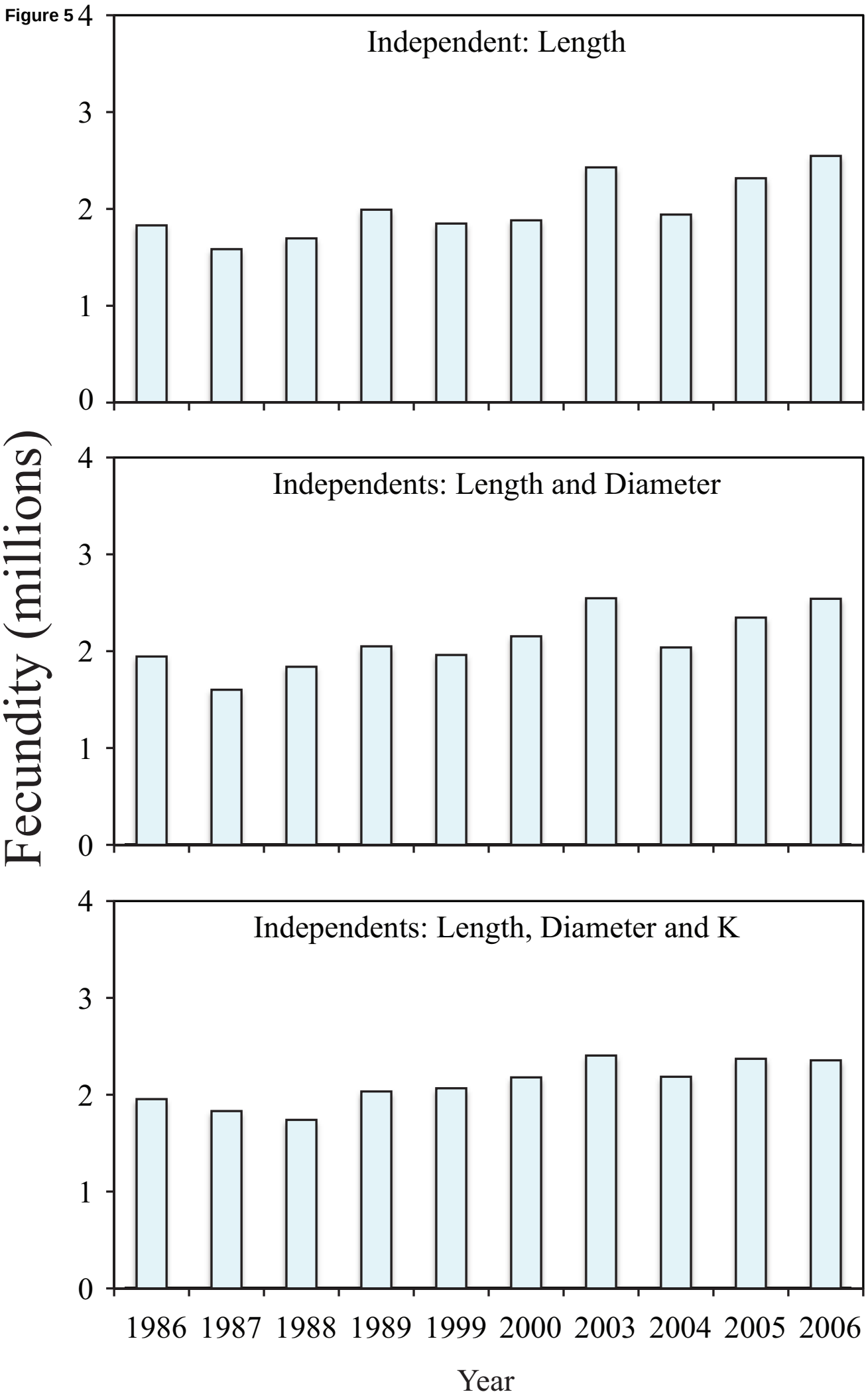
Independent: Length
Independents: Length and Diameter
Independents: Length, Diameter and K
Fecundity (millions)
0
1
2
3
4
1986
1987
1988
1989
1999
2000
2003
2004
2005
2006
Year

Figure 64

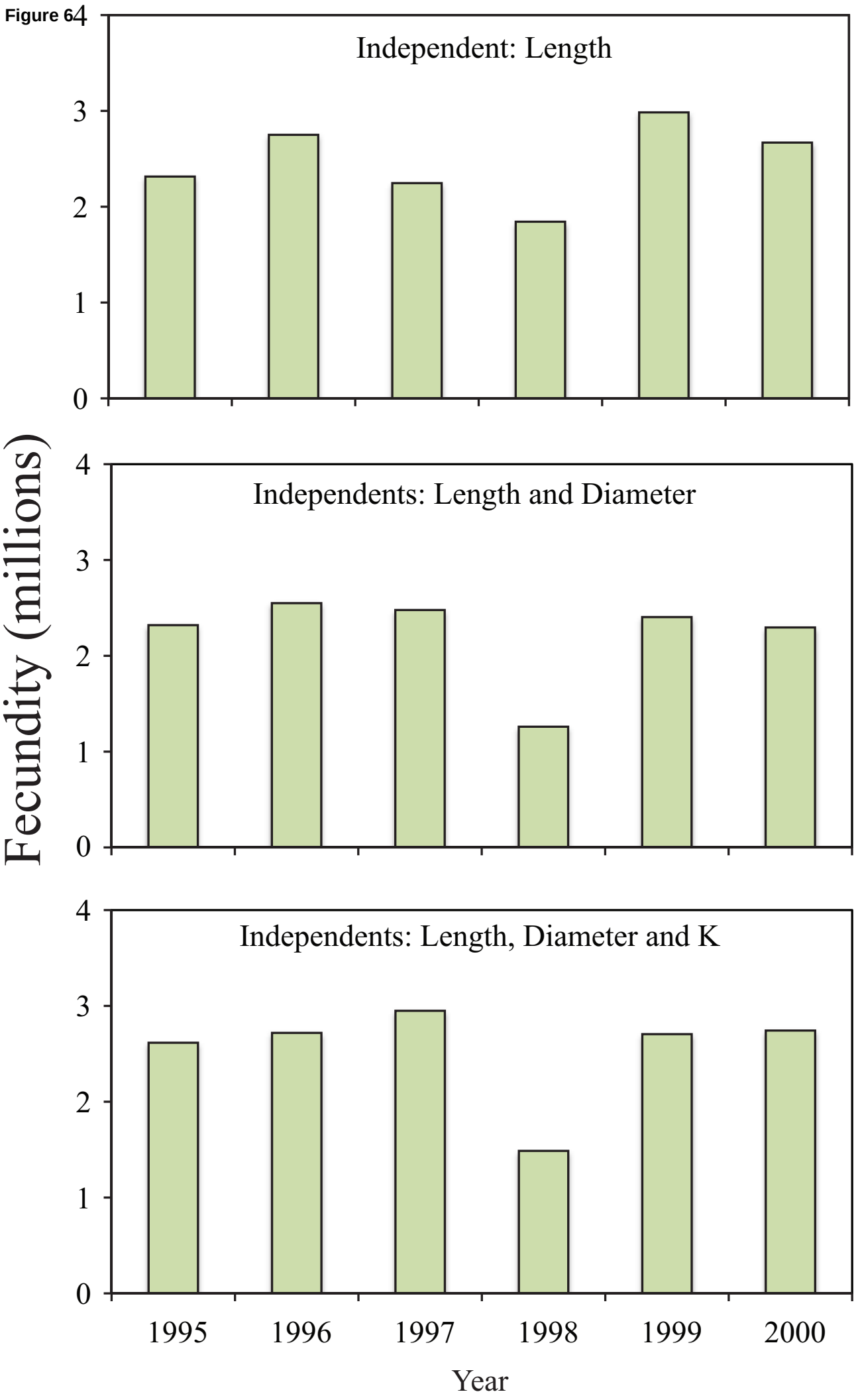
Independent: Length
Independents: Length and Diameter
Independents: Length, Diameter and K
Fecundity (millions)
0
1
2
3
4
1995
1996
1997
1998
1999
2000
Year

Figure 7

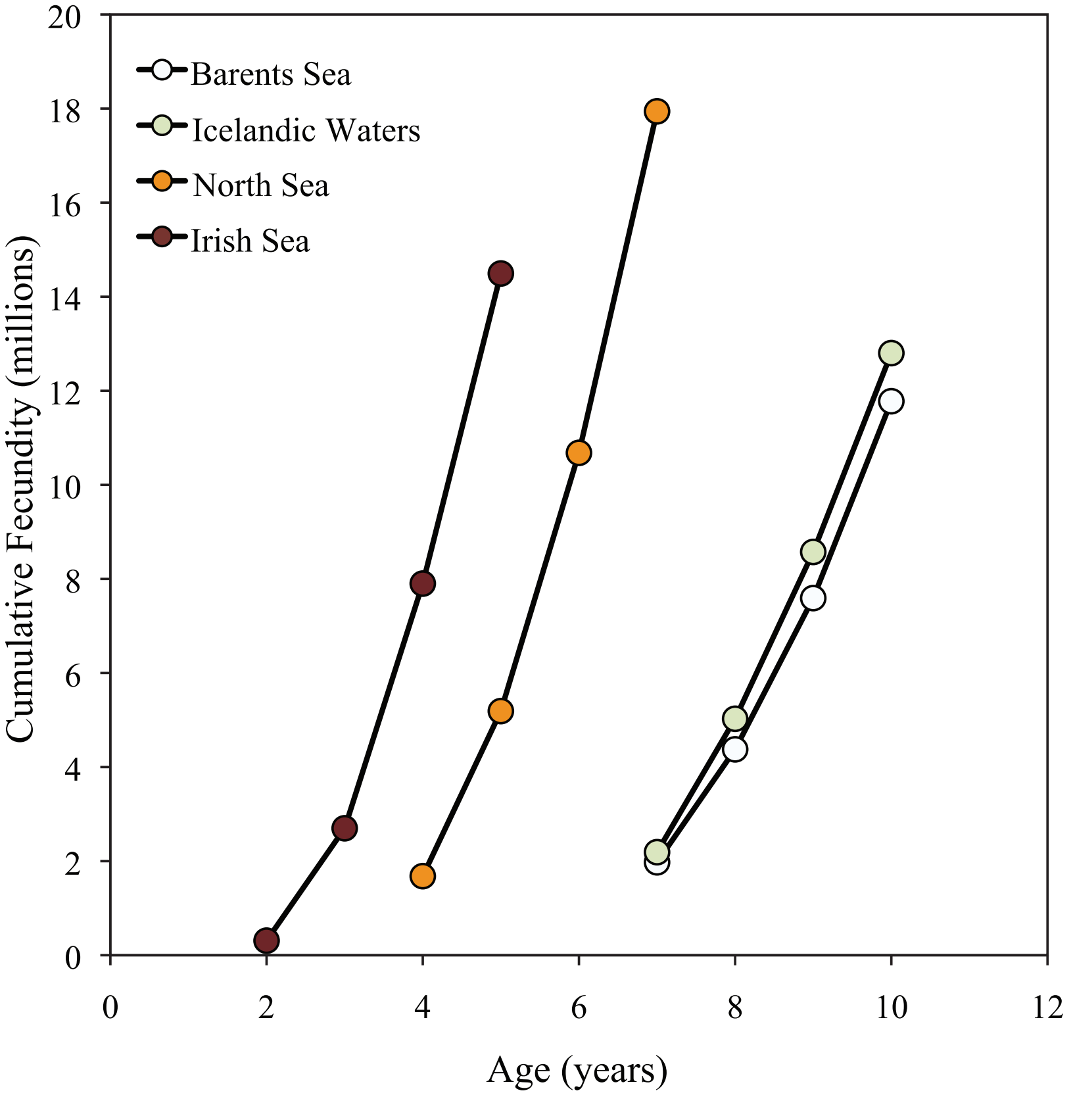
Barents Sea
Icelandic Waters
North Sea
Irish Sea
Cumulative Fecundity (millions)
Age (years)
0
2
4
6
8
10
12
14
16
18
20

Table 1. Length, condition, and mean oocyte diameter for the sampled fish.

			Fulton´s K				Length (cm)				Mean oocyte diameter (µm)			
Stock	**Year**	**N**	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Barents Sea														
	1986	29	0.90	0.126	0.67	1.21	81.8	15.4	55.0	122.0	646	69	467	789
	1987	20	0.73	0.094	0.57	0.91	64.1	8.3	52.0	82.0	679	71	444	784
	1988	49	0.89	0.094	0.73	1.21	79.6	19.4	50.0	122.0	681	64	532	799
	1989	110	0.90	0.084	0.64	1.14	84.5	22.1	50.0	126.0	619	62	465	763
	1999	90	0.87	0.066	0.71	1.04	85.2	9.7	67.5	121.0	648	62	469	813
	2000	79	0.89	0.078	0.75	1.16	80.8	9.4	57.0	101.0	692	62	548	832
	2003	48	0.95	0.095	0.78	1.17	84.9	14.7	58.5	117.0	629	71	468	773
	2004	51	0.87	0.105	0.68	1.09	86.1	16.1	63.0	121.0	627	51	502	744
	2005	45	0.91	0.113	0.74	1.27	89.7	13.4	63.0	123.0	620	68	408	726
	2006	78	0.95	0.108	0.71	1.38	86.2	16.9	54.0	120.0	603	73	373	715
	Total	**599**	**0.89**	**0.060**	**0.73**	**0.95**	**82.3**	**7.0**	**64.1**	**89.7**	**644**	**30**	**603**	**692**
Icelandic Waters														
	1995	263	1.08	0.16	0.46	1.49	94.2	11.9	67.0	125.0	619	56	477	786
	1996	159	1.06	0.18	0.73	1.59	91.1	18.2	57.0	133.0	567	70	423	766
	1997	141	1.13	0.19	0.80	1.60	95.9	11.4	67.0	128.0	696	74	519	849
	1998	92	1.03	0.14	0.68	1.35	98.1	15.7	59.0	129.0	493	64	380	675
	1999	101	1.05	0.17	0.75	1.46	94.4	18.2	59.0	133.0	509	73	355	721
	2000	96	1.00	0.17	0.72	1.57	87.6	15.0	63.0	131.0	534	74	407	782
	Total	**852**	**1.06**	**0.04**	**1.00**	**1.13**	**93.6**	**3.7**	**87.6**	**98.1**	**570**	**76**	**493**	**696**
North Sea														
	2003	42	1.12	0.15	0.87	1.74	68.9	17.9	34.0	115.0	540	126	355	793
	2004	39	1.14	0.14	0.85	1.42	69.5	15.8	36.0	113.0	605	107	393	792
	Total	**81**	**1.13**	**0.01**	**1.12**	**1.14**	**69.2**	**0.4**	**68.9**	**69.5**	**573**	**46**	**540**	**605**
Irish Sea														
	2003	18	1.13	0.06	1.02	1.26	45.8	6.7	39.0	68.3	658	47	569	723
	2004	33	1.41	0.18	1.14	1.98	63.5	13.4	45.0	92.0	686	64	526	789
	Total	**51**	**1.27**	**0.19**	**1.13**	**1.41**	**54.6**	**12.5**	**45.8**	**63.5**	**672**	**20**	**658**	**686**

Table 2. Age and length at 50 % mature for the Barents Sea cod, Icelandic cod, North Sea cod, and Irish Sea cod females. Data for Icelandic cod taken from Marteinsdóttir and Begg (2002).

Stock	**Barents Sea**	**Icelandic waters**	**North Sea**	**Irish Sea**
Period	**1981-2002**	**1985-1999**	**1981-2002**	**2003-2004**
A_{50} (years)	7.2	6.6	3.8	1.6
L_{50} (cm)	78	76	62	36

Table 3. Potential fecundity regressions split by stock and year using length, mean oocyte diameter and condition as independent variables. All regressions and regression coeffecients (except mean oocyte diameter for Irish Sea cod) were significant with $P \leq 0.001$. For calculation of fecundity (F) from the regression coefficients the following equation should be used: $F = e^{a}$ Length^{b} Diameter^{c} Condition^{d}

Barents Sea

A	Total	1986	1987	1988	1989	1999	2000	2003	2004	2005	2006
Intercept (a)	-15.526	-17.049	-16.664	-16.580	-13.965	-15.364	-15.802	-13.966	-15.290	-14.343	-14.912
Length (b)	3.702	4.029	3.908	3.904	3.344	3.646	3.751	3.390	3.641	3.465	3.616
r^2	0.860	0.892	0.787	0.915	0.923	0.745	0.767	0.835	0.869	0.810	0.853

B	Total	1986	1987	1988	1989	1999	2000	2003	2004	2005	2006
Intercept (a)	-7.460	-11.822	-6.858	-11.742	-7.028	-10.071	-9.012	-6.751	-7.352	-9.822	-6.493
Length (b)	3.620	4.153	3.363	3.822	3.311	3.647	3.651	3.260	3.717	3.531	3.589
Diameter (c)	-1.193	-0.893	-1.158	-0.687	-1.058	-0.819	-0.972	-1.032	-1.286	-0.750	-1.298
r^2	0.889	0.903	0.825	0.917	0.936	0.772	0.795	0.866	0.888	0.829	0.899

C	Total	1986	1987	1988	1989	1999	2000	2003	2004	2005	2006
Intercept (a)	-6.884	-8.911	-8.188	-12.831	-6.795	-9.077	-8.499	-4.092	-3.775	-7.845	-6.980
Length (b)	3.335	3.612	3.372	3.440	3.268	3.354	3.617	2.971	3.241	3.201	3.325
Diameter (c)	-1.059	-0.951	-0.921	-0.223	-1.036	-0.731	-0.998	-1.235	-1.482	-0.807	-1.024
Condition (d)	1.620	1.383	0.793	2.264	1.626	1.917	1.617	1.301	1.410	1.324	1.576
r^2	0.937	0.942	0.850	0.964	0.963	0.861	0.873	0.899	0.926	0.895	0.944

Icelandic waters

A	Total	1995	1996	1997	1998	1999	2000
Intercept (a)	-18.305	-18.692	-17.495	-19.494	-23.294	-16.869	-18.759
Length (b)	4.386	4.457	4.223	4.633	5.455	4.099	4.505
r^2	0.832	0.805	0.909	0.746	0.837	0.877	0.859

B	Total	1995	1996	1997	1998	1999	2000
Intercept (a)	-14.524	-14.383	-13.612	-14.679	-12.301	-11.223	-12.854
Length (b)	4.544	4.573	4.462	4.725	5.504	4.313	4.702
Diameter (c)	-0.707	-0.753	-0.782	-0.800	-1.811	-1.063	-1.082
r^2	0.852	0.816	0.917	0.762	0.889	0.905	0.890

C	Total	1995	1996	1997	1998	1999	2000
Intercept (a)	-9.392	-9.518	-9.275	-7.281	-6.868	-8.520	-6.604
Length (b)	3.759	3.773	3.842	3.593	4.673	3.695	3.606
Diameter (c)	-0.968	-0.958	-1.037	-1.168	-2.081	-1.057	-1.294
Condition (d)	1.458	1.318	1.265	1.573	1.754	1.414	1.564
r^2	0.907	0.889	0.945	0.876	0.925	0.951	0.940

Table 3 continued

North Sea

A	Total	2003	2004
Intercept (a)	-13.777	-13.454	-14.343
Length (b)	3.476	3.426	3.580
r^2	0.880	0.879	0.915

B	Total	2003	2004
Intercept (a)	-8.829	-7.623	-12.556
Length (b)	3.553	3.510	3.605
Diameter (c)	-0.834	-0.987	-0.296
r^2	0.916	0.931	0.917

C	Total	2003	2004
Intercept (a)	-6.886	-5.562	-10.679
Length (b)	3.309	3.216	3.426
Diameter (c)	-1.001	-1.143	-0.492
Condition (d)	1.262	1.395	1.061
r^2	0.937	0.952	0.935

Irish Sea

A	Total	2003	2004
Intercept (a)	-15.430	-13.206	-14.881
Length (b)	3.911	3.312	3.786
r^2	0.930	0.808	0.895

B	Total	2003	2004
Intercept (a)	-13.403	-7.771	-13.886
Length (b)	3.953	3.427	3.806
Diameter (c)	-0.338	-0.906	-0.166
r^2	0.930	0.816	0.892

C	Total	2003	2004
Intercept (a)	-9.403	-6.935	-10.338
Length (b)	3.585	3.468	3.727
Diameter (c)	-0.779	-1.071	-0.746
Condition (d)	1.352	0.641	1.690
r^2	0.957	0.808	0.947

Table 4. Model output on relative fecundity (eggs g^{-1}) by stock and class. Values calculated from regression models using length and mean oocyte diameter as independent variables. For calculating output a mean oocyte diameter of 600 µm was used.

Length	Barents Sea	Icelandic waters	North Sea	Irish Sea
60 cm	416	354	615	677
90 cm	497	532	711	892
100 cm	521	591	738	